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A Preliminary Systematic Assessment of the Rudabánya Hipparions (Equidae, Mammalia)

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with 4 figures

Abstract

A small sample of hipparions from Rudabánya, Hungary, are described and analysed here. The skull, maxillary and mandibular cheek teeth show affinities with Central European *Hippotherium primigenium* s. s., whereas the posteranial skeleton is relatively more gracile and lightly built, and leads us to refer this assemblage to *Hippotherium* aff. *primigenium*, a member of the *Hippotherium primigenium* evolutionary lineage. These observations suggest that the Rudabánya fauna is later Vallesian age, but may have been somewhat endemic in character. Future work on the Rudabánya hipparion assemblage will focus on clarifying its systematic position and testing the biochronologic and biogeographic hypotheses advanced here.

Kurzfassung

Die wenigen in Rudabánya, Ungarn, gefundenen Überreste von Hipparionen werden beschrieben und analysiert. Der Schädel und die Zähne des Ober- und Unterkiefers sind denen der zentraleuropäischen Art *Hippotherium primigenium* s. s. in Gestalt und Abmessungen sehr ähnlich, während das posteraniale Skelett wesentlich graziler und leichter gebaut erscheint. Daher ordnen wir diese Funde *Hippotherium* aff. *primigenium* zu. Dies läßt vermuten, daß die Funde aus Rudabánya aus dem späten Vallesian stammen, wobei aber die Fauna dort einen teilweise endemischen Character zeigte.

Összefoglalás

A kevés Rudabányán (Magyarország) talált *Hipparion*-maradványt irja le és analizálja ez a munka. A koponya és az alsó ill. felsö állkapocs fogai méretben és alakban igen hasonlóak a középeurópai *Hippotherium primigenium* s. s. esetében ismeretes kiképzödéshez, mig a postkraniális csontváz lényegesen finomabb és könnyebb épitésü. Ezért ezeket a leleteket *Hippotherium* aff. *primigenium* néven jelöljük meg, mint a Hippotherium primigenium származási vonal egy tagját.

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Ezen tények alapján azt véljük, hogy a rudabányai fauna kora késö vallesian, bár az ottani faunaegyüttes bizonyos fokig endemikus jellegü. A jövöbeli munkát a *Hipparion*-együttes rendszertani poziciójának további tisztázására valamint az itt kifejtett biokronológiai és állatföldrajzi elméletek tesztelésére fogjuk koncentrálni.

1. Introduction

We report on a small assemblage of hipparions from Rudabánya, Hungary. Rudabánya was first discovered in 1967, and sporadically collected until 1985, when fossil hominoid primates were first discovered. Since then, further excavation has been undertaken at this locality with retrieval of a diverse mammalian fauna and flora (Kretzoi, 1969, 1974, 1975, 1976 a, 1976 b, 1984; Kretzoi et al, 1976; Kordos, 1982, 1987 a, 1987 b, 1988 a, 1988 b, 1989, 1990 a, 1990 b, 1990 c). Rudabánya is unquestionably one of the most important Hungarian Neogene localities from the standpoints of its faunal and floral diversity, stratigraphic position, and potential for diverse paleobiological studies. The Rudabánya „*Hipparion*" is significant because of the reference point it can provide for the fauna's biochronology and biogeographic connections. The sample we report was made by Kretzoi prior to 1987. Because the Rudabánya *Hipparion* collection continues to increase in size annually, we will have the future opportunity to make systematic revisions and test chronologic and biogeographic hypotheses forwarded here. This work should be taken as being preliminary.

2. Methods

We use a combination of discrete character states and measurements on continuous variables to identify hipparionine species and determine their potential phylogenetic relationships. Definition and use of discrete characters which we have adopted for the skull and mandible has developed, and has been progressively refined by Woodburne & Bernor (1980), Bernor & Hussain (1985), Bernor (1985), Bernor et al. (1988), Bernor et al. (1989), Bernor & Lipscomb (1991; in press). Investigations of postcranial anatomy and functional morphology has been developed from Tobien (1952), Sondaar (1968) and Hussain (1975). Measurements follow those prescribed by the American Museum of Natural History International *Hipparion* Conference, 1981. All measurements are in millimeters, and specific measurements follow those prescribed by Eisenmann et al. (1988).

Abbreviations:

POF – Preorbital Fossa
Ru – Rudabánya
Ma – Megannum, millions of years ago
mm – millimeters
MC III – metacarpal III
MT III – metatarsal III

hipparionine or hipparion – any horse with an isolated protocone of the maxillary premolar and molar teeth and, as far as known, tridactyl feet, including species of the following genera: *Hipparion, Neohipparion, Nannippus, Cormohipparion, Hippotherium, Proboscidipparion, „Sivalhippus", „Plesiohipparion", Eurygnathohippus (= Stylohipparion), Cremohipparion,* and *Pseudhipparion*. Characterizations of these taxa can be found in MacFadden (1984), Bernor & Hussain (1985), Webb & Hulbert (1986), Hulbert (1987), Bernor et al. (1989) and Bernor & Lipscomb (1991; in review).

„*Hipparion*" - hipparionine horses that belong to different lineages than those listed above, or which cannot be readily placed within a particular lineage.

Statistics were calculated using the software package SYSTAT 5.03 licensed to BERNOR through the Smithsonian Institutions, Washington D. C..

3. Systematic Paleontology

3.1 Systematic Perspective

BERNOR et al. (1989) have recently reviewed the phylogenetic relationships of Old World hipparionines. We follow their philosophy in seeking to characterize hipparionine species by study of skeletal morphologic character complexes, and implement morphometric analysis of continuously distributed variables to further discriminate species. Moreover, we seek to analyse hipparionine specimens from stratigraphically controlled horizons (when at all possible). We believe that identifying shared-derived morphological states between statistically demonstrable and defensible species will ultimately yield the most explicit basis for identifying phylogenetic lineages.

Order Perissodactyla OWEN 1848
Suborder Hippomorpha WOOD 1937
Superfamily Equoidea HAY 1902
Family Equidae GRAY 1821
Subfamily Equinae STEINMANN & DÖDERLEIN 1890
Hippotherium aff. *primigenium*

Lectotype – Right fragmentary mandible with P2–4 from Eppelsheim, Rheinhessen, Germany. This specimen, preserved in the Senckenberg Museum, Frankfurt, Germany, is referred by V. MEYER (1833: plates XXX–XXXI, figs. 17, 18).

Type Locality and Age – Eppelsheim, Germany; Pannonian Age (= Early Vallesian, ca. 11 Ma).

Referred Specimens – V12125, adult fragmentary skull with left canine, right canine and P2-M3; mandibular cheek teeth: V12551 – right P2 and unerupted cheek tooth, V38 – left P4, V12591 – cheek tooth fragment, no number – left P4, no number – deciduous cheek tooth fragment; metacarpal III: V12039, V11841, V11853; metacarpal IV: V12613; astragalus: V12601; calcanea: V12601 – left, V12612 – left, V12600 – fragment; metatarsal II: V11852; distal metapodial III fragmentary elements: V12562, V11965, V11972, V11853, V11812, V11814; anterior and posterior phalanges 1, digit III: V11965, V11902, V11853, V11814, no number; phalanges 2, digit III: V12600, V12589, V12077a and b, V11975; phalanges 1, digits II or IV: V11893, no number.

– Geographic Range – Central Europe (= Central Paratethys Bioprovince of RÖGL and STEININGER, 1983 and BERNOR et al., 1988).

3.2 Diagnosis (after BERNOR et al., 1989)

Hippotherium primigenium is a large hipparionine horse with moderate length snout; preorbital bar long (46 - 57 mm), with anterior extent of lacrimal placed more than one-half the distance from the anterior orbital rim to the posterior rim of the fossa; preorbital fossa subtriangular-shaped and anteroventrally oriented, deeply pocketed posteriorly, with great medial depth, medial wall lacking internal pits, peripheral border outline strong with a prominent anterior rim; nasal notch well anterior to P2; cheek teeth relatively low crowned, in middle stage-of-wear adults, P2–M3 length

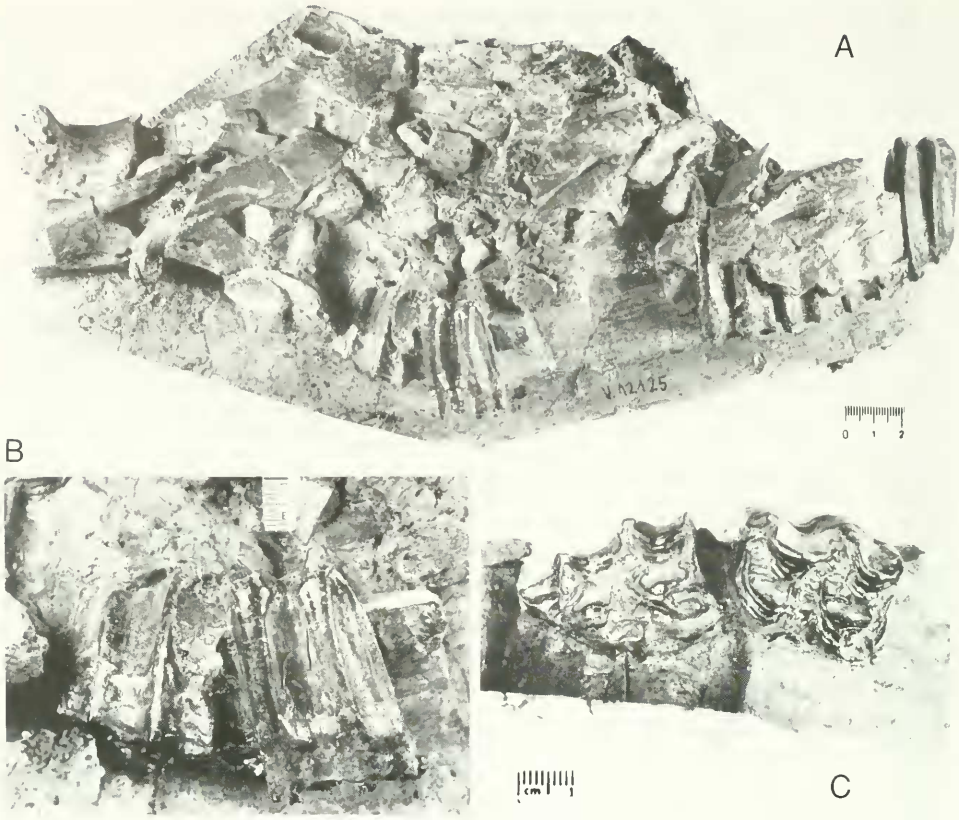


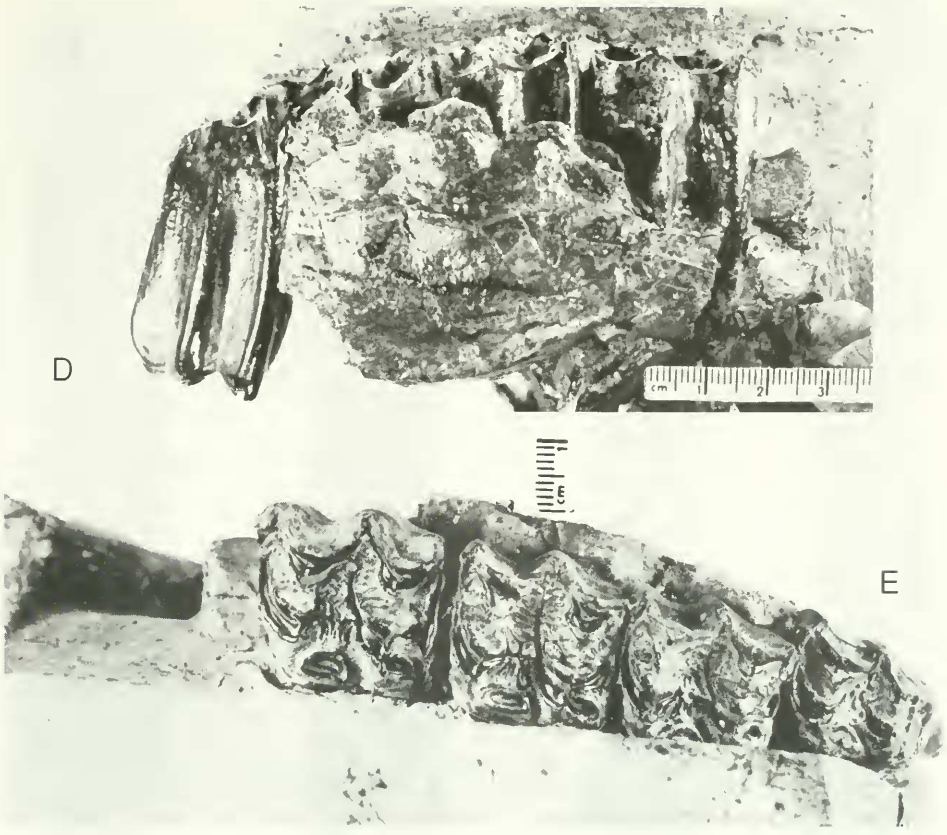
Figure 1: Skull, Ru V12125; 1A – left lateral view; 1B – left P2–3, lateral view; 1C – left P2–3, occlusal view; 1D – left P4 – M3, lateral view; 1E – left P4–M3, occlusal view.

dimension usually between 155 mm and 165 mm, fossette ornamentation complex, pli caballins bifid or complex, hypoglyphs deeply incised, protocones usually lingually flattened and labially rounded and P2 anterostyle elongate; middle wear adult mandibular cheek teeth usually with well developed protostylids and complexly plicated enamel margins; metapodials are generally short and rather robust, metacarpals have flattened distal sagittal keels, and the facet for the hamate/magnum articulation has a rather low angle (120 to 130 degrees).

3.3 Description

The skull (Figs. 1A–E) is mediolaterally crushed and includes the snout as far anteriorly as the incisor region, which is missing, the premaxilla and maxilla posteriorly, nasal notch, right and left canine, and all the left side cheek teeth. Orbits, preorbital fossa and cranium are missing, or severely distorted by crushing.

While difficult to reconstruct, the nasal notch gives the appearance of being well anterior to P2 (see Fig. 1A). The canines are large, as is typical for a male individual. The maxillary cheek teeth (Figs. 1B-1E; measurements, Table 1) are in a relatively early stage-of-wear, with details of the occlusal



morphology well developed on all teeth except M3, which is in a somewhat early stage-of-wear. Maximum crown height is measurable on M3, and equals 45.4 mm (note however because of the strong curvature of M3, the maximum crown height of an equivalent wear-stage, straight-walled P4 or M1 would have been greater, ca. 50+ mm). All cheek teeth exhibit complexly plicated, thick enamel bands of the pre- and postfossettes; complex pli caballins (often clearly having more than 2 plis); hypoglyphs are very deeply incised, nearly encircling the hypocone; protocone shows some variability due to different stages of wear amongst the teeth: P2 has an elongate oval shape (= North American *Cormohipparion* morphology of BERNOR et al., 1988), P4 has lingually flattened and labially rounded morphology, while the molars have a more buccolingually compressed morphology. The variability of maxillary cheek tooth morphology seen here is typical for earlier stages of wear; a middle stage-of-wear yields more uniform morphologies. P2 has an elongate and narrow anterostyle.

There are a number of mandibular cheek teeth present (see Table 2). Maximum height of these is recorded in an unerupted, but fully formed P4: 52.0 mm. This tooth best approximates the maximum crown height for this horse. Occlusal morphology is developed only on Ru V12551 and Ru V38. These teeth exhibit rounded metaconids and metastylids, shallow linguaflexids, ectoflexids shallow and not separating metaconid and metastylid, entoflexids with very complex borders, pli caballinids present and protostylids present, but not columnar in morphology.

This assemblage's postcranial skeleton includes three metacarpal III's (Table 3; +Figs. 2A and B), one metacarpal IV (Table 4B), one astragalus (Table 5; Figs. 3A and B), two calcanea fragments

Figure 2: Metacarpal III, Ru V12039, Metatarsal III, Ru V 12538; 2A–MC III, Ant. view; 2B–MC III, Post. view; 2C – MT III, Ant. view; 2D – MT III, Post. view.

(Table 6), one metatarsal III (Table 7; Figs. 2C and D), one metatarsal IV (Table 8), six unidentifiable distal metapodial III elements (Table 9), five posterior 1st phalanges digit III (Table 10), five anterior and posterior 2nd phalanges digit III (Table 11) and anterior or posterior 1st phalanges of digits II or IV (Table 12).

While this sample of posteranial remains is small, it compositely shows some interesting morphological attributes. Figure 4A projects a 95% confidence ellipse for the Höwenegg population of *Hippotherium primigenium* MC III's distal articular width (M 11) versus maximum length (M 1) compared to other Vallesian members of the *Hippotherium primigenium* evolutionary lineage (sensu Bernor & Lipscomb, in review). The dimensions for Ru V12589 are indicated by a symbol

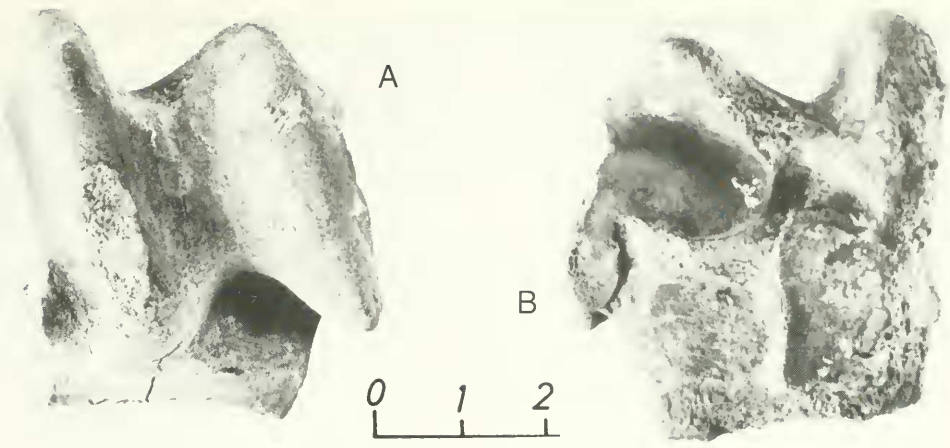


Figure 3: Astragalus, Ru V12601; 3A – dorsal view; 3B - ventral view.

positioned just outside the upper left-hand portion of the ellipse, revealing its (as well as one individual from Esme Akçaköy, Turkey) relatively long and slender dimensions. Figure 4B projects a 95% confidence ellipse for the Höwenegg population MT III's distal articular width (M 11) versus maximum length (M 1) dimensions, again compared to other members of the *Hippotherium primigenium* evolutionary lineage. Ru V12038, an MT III, shows even greater lengthening, well outside the Höwenegg 95% confidence ellipse, and is only exceeded by a single individual (of two) from Nombrevilla, Spain (after SONDAAR, 1961). Figure 4C plots mediolateral (M 4) versus dorsoventral (M 5) dimensions for the Höwenegg horse proximal calcaneum (calcaneum tuber; Ru V12600). Quite a different pattern is revealed here in that the Rudabánya calcaneum is relatively small in dimension. Figure 4D plots astragalus maximum length (M 1) versus its maximum mediolateral dimension (M 4). Here, the smaller size of the Rudabánya astragali (Ru V12601 R-3-R and Ru V1261) is even more convincingly demonstrated.

3.4 Remarks

Because of the limited size of this Rudabánya sample, conclusions about the morphology, systematics, age and biogeography should be considered to be preliminary. Morphologically the skull, maxillary and mandibular dentition are virtually identicle to the Höwenegg hipparion. Moreover, BERNOR & LIPSCOMB (in review), referring to Rudabánya material not yet published, note that mandibular cheek tooth metaconids and metastylids show squaring in a significant percentage of the specimens, as is found with the Höwenegg horse. The metapodials, especially MT III, are longer and more slender, and the calcaneum and astragali are smaller than the Höwenegg horse, and most other representatives of the *Hippotherium primigenium* evolutionary lineage. The posteranial morphology suggests a more gracile-limbed horse than seen in the Höwenegg horse, and more primitive members of the lineage.

While sharing a number of primitive characters of the skull and dentition, the Rudabánya horse's variable rounding/squaring of the lower cheek tooth metaconids and metastylids, lengthening of the metapodials, especially MT III's, and decrease in size of limited tarsal elements, all suggest an

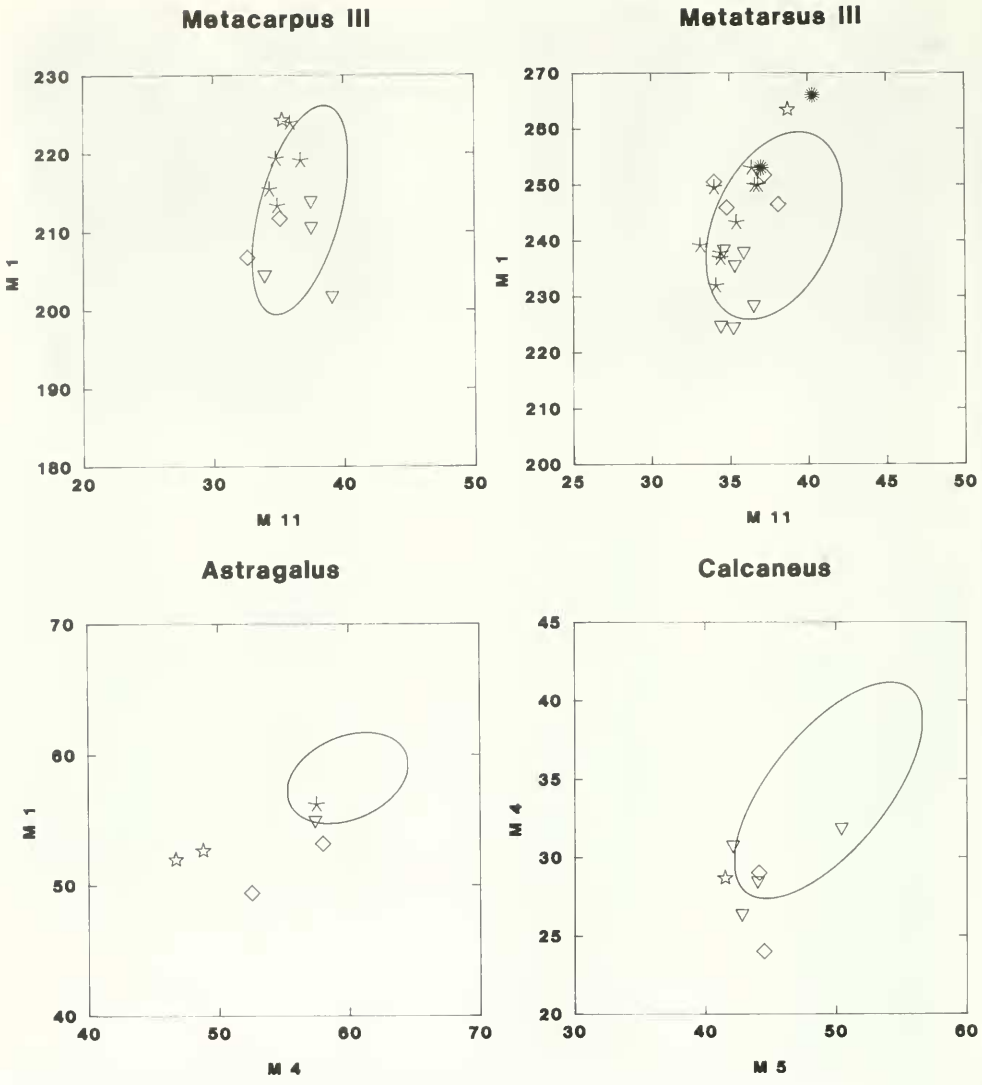


Figure 4: Bivariate plots comparing 95% ellipse for Höwenegg horse range of variability versus measurement for Rudabánya horse; 4A – Ru V12039: MC III measurement 11 (distal articular width) versus measurement 1 (maximum length); 4B – RU V12038 MT III measurement 11 (distal articular width) versus measurement 1 (maximum length): 4C – Astragalus measurement 1 (maximum length) versus measurement 4 (maximum breadth); Calcaneus, measurement 5 (proximal maximal depth) versus measurement 4 (proximal maximal breadth).

☆ Rudabánya,

▷ Inzersdorf,

✶ Esme Akçaköy,

◇ Charmoille,

✹ Nombrevilla.

evolved condition over the Höwenegg horse. BERNOR & LIPSCOMB (in review) have argued that Höwenegg does not represent the most primitive member of the *Hippotherium primigenium* evolutionary lineage. Rather, they argue that the phylogeny of this group suggests the following biochronological ranking of Central European Vallesian *Hippotherium primigenium* (from oldest to youngest yet analysed by BERNOR): Pannonian C population of the Vienna Basin – Pannonian D–E (Vienna Basin) and Eppelsheim (Germany) population – Nombrevilla (Spain) – Höwenegg (Germany) – Rudabánya.

Whereas BERNOR et al. (1988) have argued that the Vienna Basin „*Hipparion*" Datum stratigraphically occurs in uppermost Pannonian Zone B or lowermost Zone C, and second order correlations suggest an age of 11.5-11 Ma, SEN (1989) and BERNOR et al. (1989) cite that all current evidence suggests a European „*Hipparion*" Datum no greater than 11.5 Ma, whereas the Indian Subcontinent and Subsaharan records appear to have somewhat later regional first occurrences of hipparion (ca. 9.5 and 10 Ma., respectively). These ages are currently being tested at Höwenegg, Bou Hanifia (Algeria) and Esme Akcaköy, using the single crystal laser-fusion Ar/Ar dating methodology (SWISHER, in progress).

Biogeographically, the Rudabánya horse shows its closest alliance with Central and Western Paratethys bioprovince populations of *Hippotherium primigenium*. It contrasts strikingly with the peri-Mediterranean populations of hipparions which have been shown to have rapidly diversified into new clades in response to increased seasonality (BERNOR et al., 1990). The Rudabánya fauna is well known for its diverse and endemic ape assemblage and overall warm, mesophytic forest character. Because of the apparent unique morphological pattern demonstrated for the Rudabánya hipparion, it may have been an endemic form. Future studies of the Rudabánya hipparion will attempt to clarify these preliminary hypotheses.

4. Conclusions

Our morphological and statistical analysis of the Rudabánya hipparion lead us to provisionally assign this assemblage to *Hippotherium* aff. *primigenium*. If future work on an increased sample size of postcranial elements confirms the morphological and metrical patterns given here, designation of a new species may be warrented. Chronologically, the locality's hipparion suggests a later Vallesian age for the Rudabánya fauna. The age of various Central European *Hippotherium primigenium* populations cited here will ultimately depend upon establishing an independent chronology as much as possible.

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TABLE 1. MEASUREMENTS ON RUDABANYA MAXILLARY CHEEK TEETH

1) Ru V12125

Element	Length	Width	Height	PRO	FOSS			
				L	Pre		Post	
					A	P	A	P
Lt. C	13.7	8.8	11.1					
Rt. C	12.2	23.8	35.9					
p^2	34.4			8.2	4	2	4	2
p^3	27.3	43.1	7.4		5	4	4	1
p^4	28.3		44.3	7.2	5	4	5	2
M^1	24.9			7.5	3	6	8	5
M^2	25.0			6.9	5			
M^3	24.4		45.4	6.0				

TABLE 2 MEASUREMENTS ON RUDABANYA MANDIBULAR CHEEK TEETH

Specimen No.	Element	Length	Width	Height
1) V12551 (rt.)	P_2	28.9	12.9	26.4
2) V38 (left)	P_4	25.1	13.1	21.5

TABLE 3 MEASUREMENTS ON RUDABANYA METACARPAL III's

Specimen No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1) V12039 (26/m) (lt.)	224.3	219.6	27.4	21.9	33.6		39.0	9.7		38.0	35.3	29e	23.0			
2) V11841 (25/2) R2 (lt.)					38.2	29.7	33.6	11.5								5.2
3) V11853 (25/47) R-1 (rt.)					37.4	29.6	33.0	11.2								5.3

TABLE 4 MEASUREMENTS ON RUDABANYA METACARPAL IV

Specimen No.	1	2	3	4	5	6
1) V12613 (rt.)			18.7	14.4		

TABLE 5 MEASUREMENTS ON RUDABANYA CALCANEA

Specimen No.	1	2	3	4	5	6	7	
1) V12601 R-3-A (lt.)	52.0	49.8	26.1	46.7		29.1	41	(estimate)
2) V12612 (lt.)	52.7	51(e)	26.0	48.8	42.1	28.5	40 (e)	
3) V12600			18.7	28.7	41.5			

TABLE 6 MEASUREMENTS ON RUDABANYA METATARSAL III

Specimen No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1) V12038 (26/2) (lt.)	263.5	260.2	32.2	28.4	41.2		240.2			40.8	38.7	32.2	25.0	30.0

TABLE 7 MEASUREMENTS ON RUDABANYA METATARSAL II

Specimen No.	1	2	3	4	5	6
1) V11852 R-1 (26/4) (right)			13.2	18.5		

TABLE 8 MEASUREMENTS ON RUDABANYA METAPODIAL III DISTAL ELEMENTS

Specimen No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1) V12562 (26/11) R-2											38.7	34.7	29.0	30.0	
2) V11965 (26/14) R-2										35.3	32.8	25.9	21.4	23.1	
3) V11972 (26/14) R-2										40.8	37.3	30.3	24.8	28.3	
4) V11853 (26/4) R-1											34.7	26.3	22.2	26.0	
5) V11812 (24/13) No. R										40.3	40.3	30.9	26.8	29.3	
6) V11814 (24/13) No. R										39.8	35.2	30.5	25.3	28.3	

TABLE 9 MEASUREMENTS ON ANTERIOR AND POSTERIOR PHALANX 1, DIGIT III

Specimen No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1) V11965 (26/14) R-2	58.7	55.9	28.1	38.9	29.7	29.5	27.2	16.8	25.6	40.7	39.7	16.9	19.2		
2) V11902 (26/) R-1	59.5	57.7	25.7	35.7	26.0	28.0	27.3	15.5							
3) V11853 (25/4) R-1	69.7	66.9	27.5	40.2	31.3	32.2	33.1	33.0	19.2	54.1	52.4	15.2	16.1		
4) V11814 (24/137) No. R	59.3	52.9	28.5	40.0	30.4	31.5	29.7	18.5	22.6	41.8	39.2	16.2	20.1		
5) No. Numb.	61.0	55.2			31.4										

TABLE 10 MEASUREMENTS ON RUDABANYA PHALANGES 2, DIGIT III, ANTERIOR AND POSTERIOR

Specimen No.	1	2	3	4	5	6
1) V12600 V12637 (26/12) R-3-C	41.6	31.4	31.7	42.4	29.5	35.7
2) V12589 (26/11) R-3	41.4	32.5	30.2	40.7	27.3	36.6
3) V12077 a (26/1) R-2				36.8	26.0	
4) 12077 b (26/1) R-2	42.5	31.7	27.4	37.9	26.7	30.0
5) V11975 (26) R-2	40.1	32.6	29.8	38.7	25.4	35.1

TABLE 11 MEASUREMENTS ON RUDABANYA PHALANGES 1, DIGITS II OR IV

Specimen No.	1	2	3	4	5
1) No number (26/11)	35.7	10.9	16.0	10.3	8.0
2) V11894	37.4	15.6	22.4	13.0	10.3